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A NEW PLESIADAPIFORM (MAMMALIA: PLESIADAPIFORMES) FROM THE EARLY EOCENE OF THE BIGHORN BASIN, WYOMING

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ABSTRACT

Dentaries of a very small, specialized plesiadapiform from the lower Eocene Willwood Formation are the basis for a new genus and species, *Picromomys petersonorum.* It was the smallest known plesiadapiform, weighing only about 10 g. Like some other plesiadapiforms, the new taxon has a strongly procumbent, hypertrophied medial incisor, followed by very reduced dentition between the incisor and P_4. Unlike all other plesiadapiforms, it has a unique semimolariform P_4 reminiscent of M_1 in picrodontids, as well as lower molars bearing an accessory trigonid cusp anterobuccal to the protoconid. The closest known relative of *Picromomys* appears to be Bridgerian *Alveojunctus,* and we group these two genera here in the new family Picromomyidae. Picromomyids share derived similarities with several plesiadapiform families but are probably most closely related to either Micromomyidae or uintasoricine Microsyopidae.

INTRODUCTION

Field work in early Wasatchian strata of the Willwood Formation of the Bighorn Basin in 1994 yielded dentaries of a highly distinctive new plesiadapiform. The new form is unusual in several respects, including a highly modified lower fourth premolar, presence of an accessory trigonid cusp on M_{1-2}, and its extremely small size. It also shares numerous derived traits with various plesiadapiforms assigned to four different families, but there is no compelling evidence to support a special relationship to any one particular family. Hence homoplasy must account for many of the similarities. The only strongly supported relationship is to the poorly known Bridgerian species *Alveojunctus minutus,* and even this alliance is based on very limited evidence. The latter has been considered to be a uintasoricine microsyopid (Bown, 1982; Gunnell, 1989), but its apparent similarities to microsyopids could well be convergent, for it also shares potential synapomorphies with other families. The new taxon and *Alveojunctus* are here placed in a new family of plesiadapiforms because of their unusual specializations and the lack of an unequivocal relationship to any known family of plesiadapiforms.

Recognition of new species of fossil mammals from the lower Eocene Willwood Formation is not unusual, despite more than a century of field work in these strata. Discovery of new genera or families, however, is considerably rarer. It

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serves as a reminder that we still have much to learn about mammalian diversity during the Wasatchian—even in well-studied sequences.

Abbreviations used in text are: AMNH, American Museum of Natural History, New York, New York; USGS, US Geological Survey, Denver, Colorado; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; YPM-PU, Peabody Museum, Yale University, New Haven, Connecticut.

SYSTEMATIC PALEONTOLOGY

Order Plesiadapiformes Simons and Tattersall, *in* Simons, 1972
Picromomyidae, **new family**

Type Genus.—*Picromomys,* new genus.

Included Genera.—Type genus and *Alveojunctus.*

Distribution.—Wasatchian–Bridgerian (early–middle Eocene) of Wyoming.

Diagnosis.—Diminutive plesiadapiforms having the following combination of features: very low-crowned lower molars with shallow hypoflexids, low and anteriorly canted trigonids, and hypoconulids shifted towards entoconids but separated by a distinct entoconid notch; P_4 larger than M_1 and with open, anteriorly canted trigonid and large, squared talonid with fully buccal cristid obliqua and no hypoflexid; anterobuccal cingulids poorly developed or absent.

Discussion.—Although *Picromomys* and *Alveojunctus* are extremely rare and their known fossils very fragmentary, they share several unusual features that suggest close relationship. Moreover, they are dentally so distinctive that they cannot reasonably be assigned to any named family. No other plesiadapiforms have modified P_4 in the same way. Nonetheless, there can be little doubt that both are plesiadapiforms (see Discussion following description of the new species), and there are derived resemblances to members of four different families: Micromomyidae, Microsyopidae, Picrodontidae, and Paromomyidae (see below). In no case are the similarities very compelling, however, and the likelihood that most of them result from convergence is equally plausible.

It is possible that more complete material will strengthen the alliance of Picromomyidae with one of those families—most probably Micromomyidae or Microsyopidae, to judge from present evidence—and eventually warrant reclassification (e.g., as a subfamily of Micromomyidae or a tribe of Uintasoricinae). However, family level separation seems justified by the kind and extent of dental apomorphies present in picromomyids. Many plesiadapiforms exhibit modifications of antemolar teeth while retaining rather conservative molars. In particular, a specialized, usually hypertrophied P_4 characterizes several plesiadapiform families (viz. Carpolestidae, Paromomyidae, Micromomyidae), each of which has modified this tooth in a different manner. The defining specializations of picromomyids are comparable to any of these.

Bridgerian *Alveojunctus* is known from only a small number of isolated teeth (Fig. 1) representing two or three loci, P_4, M_2(?), and possibly M_3. The single molar (the holotype) known from the Aycross Formation was identified as M_1 by Bown (1982), but in comparison with the new species appears more likely to be M_2. As noted by Bown, an M_3 from the early Bridgerian Cathedral Bluffs Tongue (Wasatch Formation, Green River Basin), referred to cf. *Niptomomys* sp. by West and Dawson (1973), may also belong to *Alveojunctus.* These two molars are distinctive and differ from those of the new species in uniquely having the trigonid basin conjoined with the talonid basin through a deep trigonid notch. P_4 of *Al-*

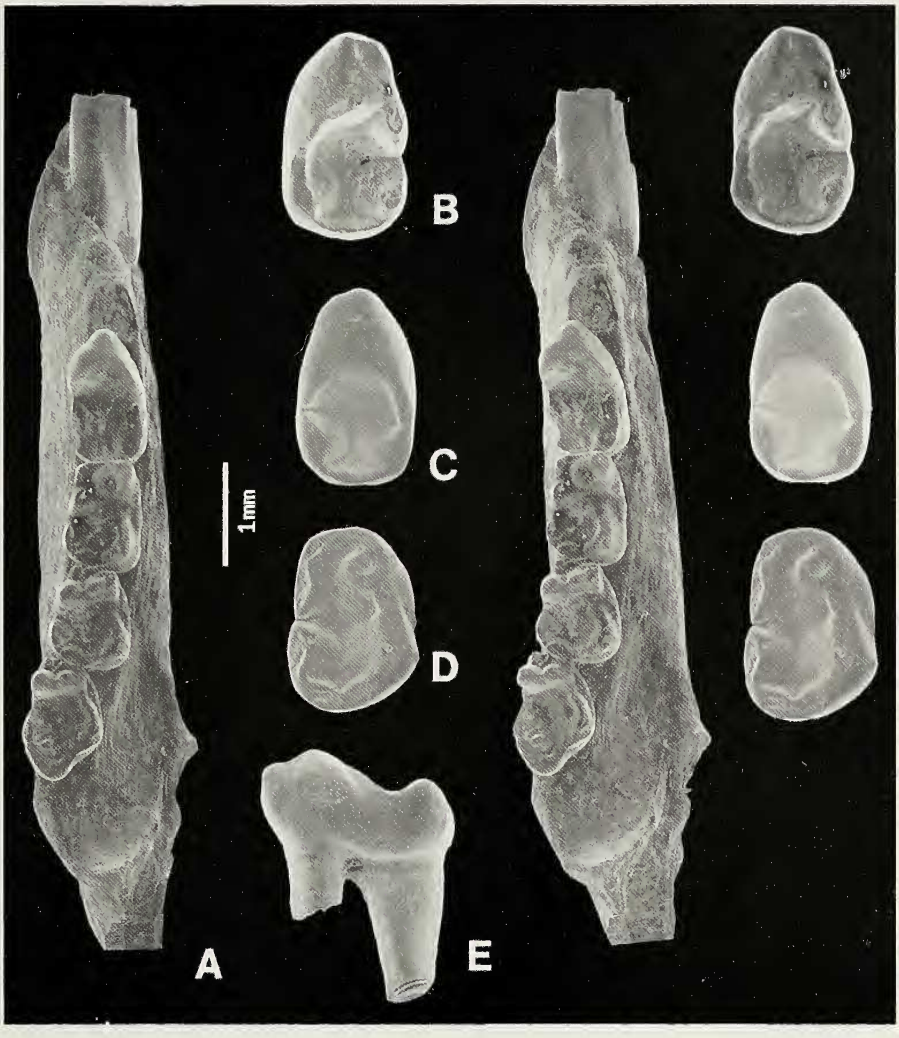

Fig. 1.—SEM stereopairs of picromomyids. A, *Picromomys petersonorum,* n. gen. and sp., holotype (USNM 487900), right dentary with base of I_1 and P_4–M_3 in occlusal view. B–E, *Alveojunctus minutus.* B, unworn left P_4 (USNM 250589); C, worn right P_4 (USNM 251446); D, right M_2?, holotype (USGS 2005); B–D in occlusal view. E, left P_4 (USNM 250589) in buccal view.

veojunctus differs from that of the new species in having a talonid with a clear basin and a particularly prominent entoconid, which is often swollen into the basin.

Picromomys, new genus

Type and Only Known Species.—*Picromomys petersonorum,* new species.

Diagnosis.—Very small plesiadapiform (M_1 length = 1.1 mm, just over half the linear dimensions of *Alveojunctus*) with enlarged, nearly horizontal medial incisor and only two small teeth between I_1 and P_4. Differs from *Alveojunctus*

and all other plesiadapiforms in having a prominent cusp-like expansion on M_{1-2} anterobuccal to the protoconid. P_4 trigonid with poorly defined blunt cusps. P_4 talonid about same length as trigonid and wider than trigonid, as in *Alveojunctus*; and flat (without basin), sloping posterolingually, and lacking distinct hypoconulid and entoconid, all in contrast to *Alveojunctus*.

Distribution.—Wasatchian (early Eocene) of Wyoming.

Etymology.—Greek *pikros,* bitter, in allusion to the superficial resemblance of P_4 to the first lower molar of Paleocene *Picrodus,* + *Omomys,* middle Eocene primate and suffix commonly used for small primitive primates and plesiadapiforms.

Picromomys petersonorum, new species
(Fig. 1, 2)

Holotype.—USNM 487900, right dentary with P_4–M_3, base of I_1, and two alveoli between incisor and P_4; left dentary with base of I_1, incomplete P_4, and all other alveoli. Only known specimen; collected by T. M. Bown in 1994. The two dentaries are assumed to represent the same individual because they are the same size, are similarly worn, and were found together in situ during quarrying, within about 1 cm of each other.

Locality and Horizon.—A stage 1 paleosol in meander-belt mudstones at USGS locality D-2035 in the Dorsey Creek badlands, SE ¼ Sec. 12, T.50 N., R.95 W., Big Horn County, Wyoming; 390 m-level of the Willwood Formation, early Wasatchian. See Bown and Kraus (1987) and Bown et al. (1994) for further information on Willwood sediments and stratigraphy.

Diagnosis.—As for genus.

Etymology.—For Ted and LaDean Peterson of Worland, Wyoming, in recognition of years of friendship and generous assistance to our expedition.

Description.—The dentary appears relatively deep because of the very low-crowned molars, but it is actually comparatively shallower than in some paromomyids. Two mental foramina are present, the larger one positioned below the front of P_4 and the other under the trigonid of M_1. The cheek tooth row is not perfectly straight in superior view, but forms a gentle arc directed slightly mediad at the posterior end, a common configuration in plesiadapiforms.

The lower dentition consists of a hypertrophied, procumbent anterior tooth, assumed to be I_1, and six postcanine teeth. The base of I_1, present in both dentaries, is oriented essentially horizontally; the crowns of both are missing. The limited portion preserved, however, provides significant information bearing on the affinities of *Picromomys.* The tooth is laterally compressed, with an elliptical cross section that is almost flat medially and convex laterally. A faint horizontal ridge is present on the anterolateral aspect near the broken edge of I_1, whereas the dorsal aspect is smoothly rounded. The preserved part of the incisor approximates that of paromomyids and micromomyids more closely than that of other plesiadapiforms, such as carpolestids or plesiadapids. Moreover, it is distinctly different from the diagnostic lanceolate lower incisor of microsyopids (including *Navajovius, Arctodontomys, Microsyops, Niptomomys,* and *Uintasorex*). In the latter group, the incisor has an abrupt dorsal expansion just distal to its base, and the crown is rotated medially. As a result, the homologue of the lateral crest in other plesiadapiform incisors is reoriented to form a sharp dorsal margin in microsyopids, and what was the "dorsal" surface faces medially. This sharp dorsal margin is absent in *Picromomys.*

Only two alveoli are present between I_1 and P_4, making *Picromomys* one of the most derived plesiadapiforms in terms of antemolar reduction. The dimensions and orientation of the two alveoli make it probable that they held two single-rooted teeth rather than a single, large double-rooted premolar. The first alveolus is smaller and slightly lower than the one behind, and is separated from I_1 by a short diastema. The inclined position of this alveolus suggests that it housed a somewhat procumbent tooth whose crown projected mesially over the front of its root, similar to the condition in apatemyids, carpolestids, and the micromomyid *Tinimomys,* as well as in some soricids, but not so closely appressed to I_1 as in uintasoricines. The homologies of this tooth are equivocal in *Picromomys* and several of the other taxa; here it is tentatively identified as P_2, but it could just as well be I_2 or

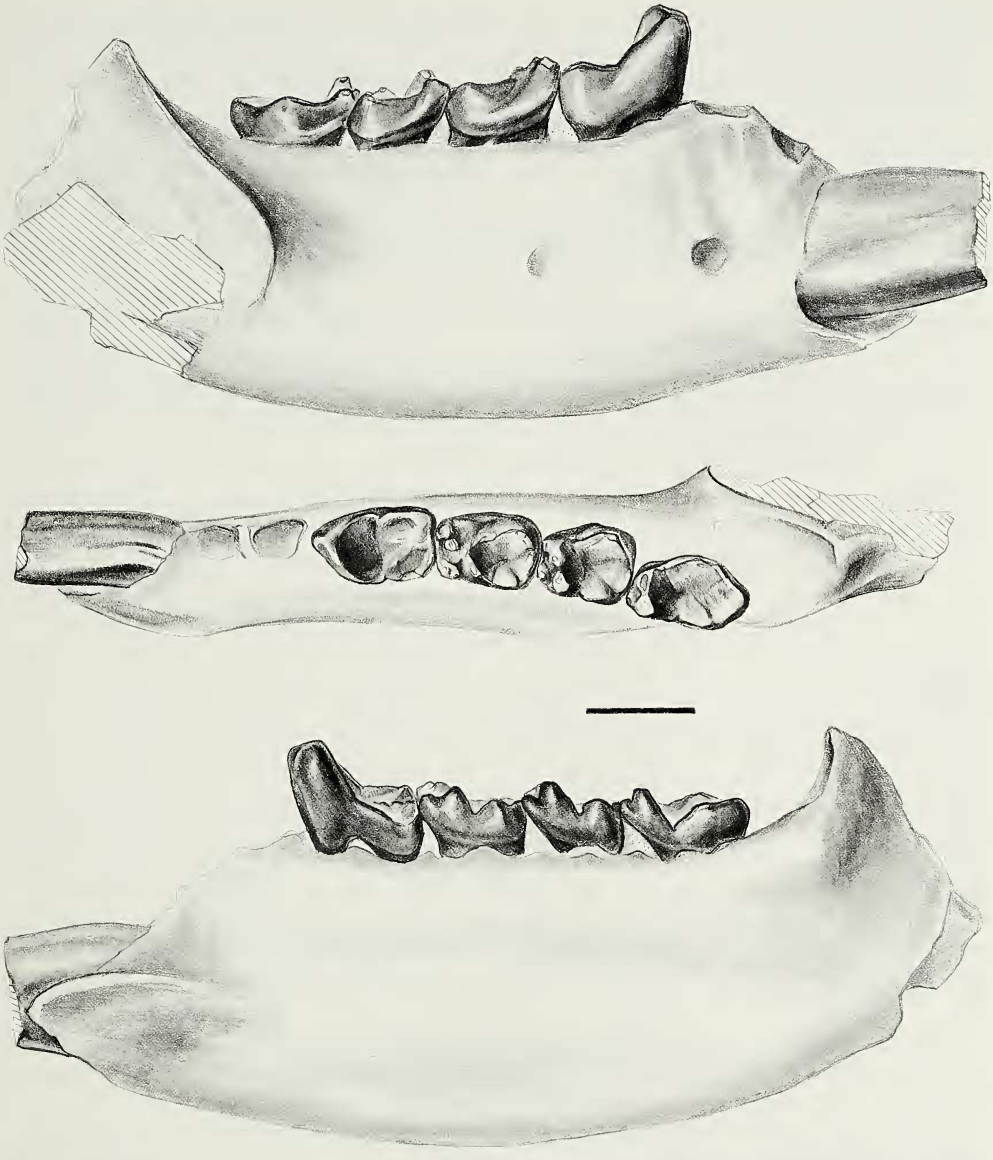

Fig. 2.—*Picromomys petersonorum,* n. gen. and sp., holotype right dentary (USNM 487900) in lateral, occlusal, and medial views. Scale = 1 mm.

the canine. The second alveolus is elliptical and somewhat larger, and probably held a tooth (P_3) with a fused double root as in *Uintasorex.*

P_4 is the most distinctive tooth and, apart from the noted resemblance to *Alveojunctus,* is unique in form among plesiadapiforms. The trigonid is tall but anteriorly canted, with a compact and wedge-shaped summit bearing blunt, ill-defined cusps or, more precisely, crests. The crests form a trefoil or Y-shaped pattern, a short anterior arm representing the paracristid, and a longer posterolingually directed arm joining an indistinct metaconid, which is indicated by a subtle swelling on the back of the trigonid. Near the midpoint (site of the protoconid?) a lower, blunt crest projects posterobuccally and merges into a sharper crest that descends the posterolateral wall of the trigonid. There it meets

the talonid just lateral to the cristid obliqua on the buccal tooth margin, producing a faint hint of a hypoflexid. The unusual appearance of the trigonid probably results from a combination of wear and weakly defined cusps, and has been interpreted in part by comparison with a series of unworn and worn P_4s of *Alveojunctus* (see Fig. 1), its closest morphological counterpart.

The talonid of P_4 is about the same length as the trigonid and is slightly broader than long. The cristid obliqua is high and fully buccal and the entocristid is much lower. These crests meet the straight postcristid at right angles, and all three crests are situated on the periphery of the talonid, barely elevated above the enclosed surface. The hypoconid, a rounded conical swelling at the posterolateral corner of the tooth, is the highest point on the talonid and the only distinct cusp. Nonetheless, it is hardly any higher than the cristid obliqua. From the hypoconid, the postcristid slopes medially to a low point at the lingual margin, where it meets the entocristid. This is normally the location of the entoconid in plesiadapiforms and other mammals that have well-developed P_4 talonids, but in *Picromomys* it is the lowest part of the talonid. From there, the entocristid ascends gradually to its highest point at the posterolingual border of the trigonid; hence, there is no talonid notch. Neither hypoconulid nor entoconid cusps are discernible, although a small bump of enamel near the hypoconid may be the remnant of a hypoconulid. Rather than having a basin, the talonid is flat. It is distinctly lower lingually than buccally, and bears an irregular fold of enamel that crosses diagonally from just inside the hypoconid to the anterolingual corner. P_4 lacks cingulids.

The lower molars are very low crowned, with trigonids that are sharply canted anteriorly and appear anteroposteriorly constricted in lateral view. Although of roughly similar dimensions, the molars increase in length in the sequence $M_2 < M_1 < M_3$. The standard trigonid cusps are bunodont, the metaconid tallest and the paraconid low and reduced, closely resembling the arrangement in *Tinimomys*. The trigonids are transversely narrow and become progressively more compressed anteroposteriorly from M_1 to M_3. The most distinctive feature of the molars is an autapomorphous cusp-like swelling, with a well-developed, beveled wear facet, situated just anterobuccal to the protoconid. It is large and columnar on M_1, somewhat smaller on M_2, and barely visible on M_3. Apatemyids also have an accessory trigonid cusp anterior to the protoconid, but the resemblance to *Picromomys* is quite superficial.

The molar talonids are increasingly broader and have increasingly deeper basins from M_1 to M_3. The talonid of M_1 is slightly longer than wide, whereas that of M_2 is wider than long. The talonid of M_3 is slightly broader still, but the third lobe is only moderately expanded, unlike the enlarged third lobe of paromomyids and plesiadapids. The cristid obliqua joins the trigonid near the protoconid on M_1 and is progressively more buccal on M_{2-3}, resulting in very shallow hypoflexids. A faint mesoconid is present on M_1. The hypoconulid and entoconid are especially prominent on M_{1-2}. The hypoconulid is lenticular or crescentic, not round or conical like the hypoconid on M_2, and is distinctly shifted toward the entoconid but separated from the latter by a distinct, shallow notch. These conditions are closely approximated in uintasoricine microsyopids (*Uintasorex* more than *Niptomomys*) and in micromomyids (especially *Tinimomys*). Unlike P_4, the molars have a well-defined talonid notch between the trigonid and entocristid. The molar ectocingulids are poorly developed, being best expressed at the hypoflexids but virtually absent anteriorly. The talonid of M_3 has weakly crenulated enamel.

Measurements (mm) of the Holotype.—P_4 length = 1.30, breadth = 0.70; M_1 length = 1.10, breadth = 0.75; M_2 length = 1.00, breadth = 0.80; M_3 length = 1.20, breadth = 0.75; depth of dentary below M_1 = 2.70.

Discussion.—With a P_4–M_3 length of 4.5 mm, the holotype belonged to an animal much smaller than any known primate, and even smaller than the diminutive micromomyid plesiadapiforms *Tinimomys* and *Micromomys* and the microsyopid *Berruvius,* up to now the smallest known plesiadapiforms. It weighed only 9.0–10.6 g, as estimated from regressions of M_1 area on body mass in all extant primates, or in prosimians, respectively (Conroy, 1987). A somewhat higher estimate, 26 g, is obtained using the regression of Gingerich et al. (1982) but, as they note, this equation overestimates the weight of insectivorous primates. Whichever regression is used, *Picromomys* apparently was no more than one-half to two-thirds the size of *Tinimomys* (Rose et al., 1993).

Picromomys resembles plesiadapiforms in several presumably derived dental traits, including presence of a hypertrophied, procumbent incisor together with low-crowned molars having reduced paraconids and broad, basined talonids. Also

like many plesiadapiforms, it is further characterized by reduction in number and size of antemolar teeth between the enlarged incisor and P_4, as well as enlargement and specialization of P_4, which has a trigonid taller than any other tooth. Although some omomyids can be similarly characterized, the combination of features in *Picromomys* conforms much more closely with that in plesiadapiforms. Thus assignment of *Picromomys* to Plesiadapiformes seems beyond doubt. The details of its dental morphology, however, indicate that *Picromomys* belongs to a clade divergent from other known plesiadapiforms. Based on the very low-crowned molars and unusual structure of P_4, the only other known member of this clade is *Alveojunctus*.

From comparisons summarized below, it will be apparent that the precise relationships and phylogenetic position of *Picromomys* and the Picromomyidae are uncertain. *Picromomys* shares numerous apparently derived dental characters, indicating potential relationship, with four known plesiadapiform clades: Paromomyidae, Picrodontidae, Micromomyidae, and uintasoricine Microsyopidae. As mentioned above, the molar trigonid arrangement in *Picromomys* is also vaguely reminiscent of that in Apatemyidae, but in the latter the accessory trigonid cusp is low and well anterior to the protoconid, forming a quadrilateral with the other trigonid cusps. There are no other compelling resemblances to apatemyids.

Phylogenetic Position of Picromomys

Cladistic analysis (using Hennig86; Farris, 1988) of 29 characters of the lower dentition in 12 plesiadapiform genera (see Appendices 1 and 2) was undertaken in an effort to resolve the relationships of *Picromomys*. The analysis yielded two equally most parsimonious trees, each with considerable homoplasy (tree length = 72, consistency index = 0.48, retention index = 0.53), one grouping picromomyids in a clade with micromomyids, and the other grouping them successively with *Niptomomys, Picrodus,* and *Ignacius* (Fig. 5). When the lanceolate incisor of microsyopids (widely considered to be an important synapomorphy of the family) was weighted 2, a single shortest tree (B) of 73 steps resulted, tree A having 74 steps under this weighting.

The two contrasting trees, and concomitant uncertain position of *Picromomys,* result in part from the very limited anatomical evidence and suggest that lower dentitions alone—at least the dental characters used in this analysis—are insufficient to establish interrelationships among plesiadapiforms with confidence. In this regard it is noteworthy that neither of the two shortest trees corroborates the widely accepted holophyly of Paromomyidae, sensu stricto (*Paromomys* and *Ignacius* in Fig. 5). Another important factor contributing to the uncertainty is the admitted ambiguity in coding several characters, usually resulting from either questionable homology (e.g., of antemolar teeth) or the inherent difficulty in coding intermediate states of continous characters. Specific ambiguities are noted in Appendix 1. The variable nature of some of the characters makes it difficult to code them consistently, and further complicates character assessment. Nonetheless, an attempt to resolve relationships on this basis is justified because the lower dentition has been the basis for much of the systematics of plesiadapiforms, and is the only evidence available for *Picromomys*; moreover, it is adequate to ascertain the uniqueness of *Picromomys*.

In both trees, *Picromomys* and *Alveojunctus* compose a monophyletic group supported by the following synapomorphies (one or both trees, indicated by A,

B, or AB): P_4 larger than M_1 (10A) and with metaconid present (27B) and talonid as long as trigonid (11AB), a buccally oriented cristid obliqua on P_4 (14AB), shallow hypoflexids (16B), low, mesially canted trigonids (17B), extreme molar brachydonty (18B), weak or absent anterobuccal cingulids (19B), moderately expressed molar paraconids (21A–reversal), and molar hypoconulids close to entoconids (28A). Only character 11(1), however, is unique to picromomyids. This combination of common traits results in a closer correspondence between these two genera than either one has with any other plesiadapiform. Even so, both *Picromomys* and *Alveojunctus* are very incompletely known, and their proposed alliance remains to be tested as the record improves.

Comparisons with Other Plesiadapiformes

Paromomyidae.—Like *Picromomys,* both *Paromomys* and *Ignacius* have relatively low-crowned molars (character 18) and broad talonids on P_4 (13). *Ignacius* further resembles *Picromomys* in having a strongly procumbent medial incisor (2), reduced anterior dentition between I_1 and P_4, a buccally oriented cristid obliqua on P_4 (14), shallow hypoflexids (16), weak molar ectocingulids (19), and low and mesially canted molar trigonids (17) (Fig. 3B, 4B). Several of these traits are also shared with *Picrodus.* Both *Picromomys* and *Ignacius* also have relatively deep dentaries, but this apparent resemblance may be exaggerated because both forms are brachydont.

As already noted, holophyly of the Paromomyidae sensu stricto is not supported by either of the two shortest trees in the parsimony analysis, but this almost certainly reflects inadequacy of the characters used here rather than lack of close relationship. In fact, two important traits, a broad, basined talonid on P_4 (13) and an expanded third lobe on M_3 (25), would support that grouping. All known paromomyids except *Paromomys* are even more derived in antemolar tooth loss than *Picromomys,* and all (including *Paromomys*) tend to emphasize crests over cusps, in contrast to picromomyids. This disparity, presumably related to a difference in diet, suggests that picromomyids and paromomyids are not very closely related.

Picrodontidae.—*Picromomys* shares several derived traits with Torrejonian *Picrodus,* including very low-crowned molars (character 18) with shallow hypoflexids (16), weak ectocingulids (19), transversely compressed trigonids (20) that are low and mesially canted (17), and variably crenulated enamel (26) (Fig. 3H, 4H). In both taxa P_3 is one-rooted (9). None of these characters is uniquely shared by these two genera, however. Also intriguing is the resemblance between the unusual enlarged cheek teeth of these two genera; but the teeth are believed to be nonhomologous (P_4 in *Picromomys,* M_1 in *Picrodus*; Szalay, 1968), and close inspection shows the similarity to be far from precise. Consequently, close relationship between picromomyids and picrodontids is unlikely, and closer probable relationships are suggested by the cladistic analysis.

Uintasoricine Microsyopidae.—Tree A indicates the Wasatchian uintasoricine *Niptomomys* as the sister taxon of picromomyids, based on the shared presence of a strongly procumbent incisor (2), P_4 with a paracristid (12[1]–reversal), a metaconid (27), and a broad but unbasined talonid (13), prominent molar hypoconulids (23–reversal), and an entoconid notch (29). These characters apply equally to Bridgerian *Uintasorex* (see Szalay, 1969), which further resembles *Picromomys* (but not *Alveojunctus*) in having a low entoconid region on P_4. Uintasor-

icines also resemble picromomyids in having very brachydont molars with very broad talonid basins. There are other derived similarities as well which are also present in successive outgroups. However, the fundamental differences in the form of P_4, the molar trigonids (transversely broad and mesiodistally compressed, with more reduced paraconids in uintasoricines), and especially I_1, together with the improbable required reversal (regeneration of a P_4 paraconid following its loss), suggest that the observed resemblances between uintasoricines and picromomyids could well be convergent.

Micromomyidae.—Micromomyids are derived, like picromomyids, in having P_4 larger than M_1 (10), transversely compressed molar trigonids (20, *Picromomys* only), and molar hypoconulids shifted toward the entoconid (28) (see Fig. 3C, D; 4C, D; and 5B, node 3). Additional derived traits found in picromomyids and *Tinimomys* (Fig. 5B, node 4), include a strongly procumbent I_1 (2), loss of several antemolar teeth (4, 6, 8), a distinct entoconid notch on lower molars (29), and a broad, basined P_4 talonid with an enlarged entoconid (13[2], 15[2], *Alveojunctus* only). *Tinimomys* and picromomyids also have similar bunodont trigonid cusps, but this resemblance is so difficult to characterize precisely that we have not included it in the cladistic analysis. Overall, these resemblances are weakly suggestive of relationship between picromomyids and micromomyids.

Characters for *Micromomys* used in this analysis were based principally on Tiffanian *M. fremdi* (Fox, 1984), the most primitive known micromomyid. In our opinion, micromomyids have been oversplit generically, and we recognize only the genera *Micromomys* and *Tinimomys* in this report. The features originally cited to distinguish *Chalicomomys* from *Micromomys* (Beard and Houde, 1989) and *Myrmekomomys* from *Tinimomys* (Robinson, 1994) do not justify their generic separation. *Chalicomomys* closely resembles *Micromomys* in its taller P_4 with much smaller talonid basin, more acute (less bunodont) molar cusps, and several other traits cited by Beard and Houde to differentiate *Chalicomomys* from *Tinimomys*. Hence there seems little reason to separate it generically from *Micromomys*. At the same time, "*Chalicomomys*" *antelucanus* strengthens the probability of a close relationship between *Micromomys* and *Tinimomys*. The putative generic distinctions of *Myrmekomomys* compared to *Tinimomys* ("relatively greater molar trigonid relief and taller talonid. . . . hypoconulid of M_{1-2} more developed;" Robinson, 1994:86) appear to vary intraspecifically in the Willwood sample of *T. graybulliensis*. The only character that differs from known samples is the more constricted hypoconulid lobe of M_3 in the holotype of *Myrmekomomys loomisi*, a feature that could be an intraspecific variant and is unlikely to warrant generic recognition. In the present study, therefore, we consider *Micromomys* to include *Chalicomomys*, and *Tinimomys* to include *Myrmekomomys*.

DISCUSSION AND CONCLUSIONS

Picromomys is a highly distinctive new plesiadapiform, demonstrably allied closely with only one other known taxon, *Alveojunctus*. These two genera are allocated to a new family, Picromomyidae, to recognize their highly distinctive dental anatomy and their ambiguous phylogenetic position among plesiadapiforms. Picromomyids possess a number of derived characters suggesting affinity with uintasoricine microsyopids, but the combination of derived resemblances supporting a relationship between picromomyids and micromomyids, especially *Tinimomys*, seems a little less susceptible to convergence and requires fewer

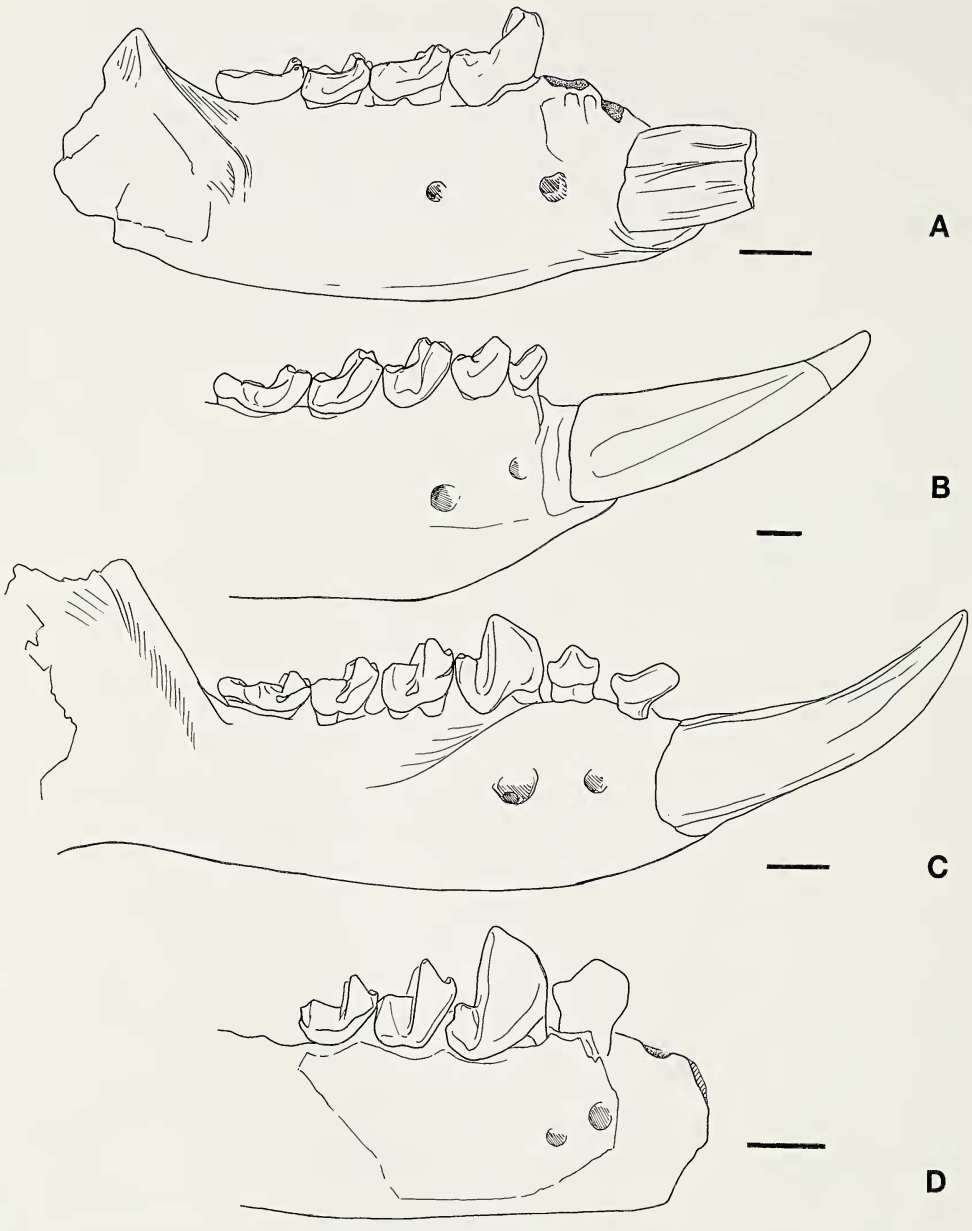

Fig. 3.—Plesiadapiform lower right dentitions in lateral view. A, *Picromomys petersonorum,* n. gen. and sp. (USNM 487900). B, *Ignacius fremontensis* (YPM-PU 14790, reversed; Paromomyidae). C, *Tinimomys graybulliensis* (after Rose et al., 1993; Micromomyidae). D, *Micromomys antelucanus* (after Beard and Houde, 1989; Micromomyidae). E, *Niptomomys doreenae* (after Rose et al., 1993; incisor restored from *N. thelmae*; Microsyopidae). F, *Navajovius kohlhaasae* (AMNH 17390, holotype, reversed; Microsyopidae). G, *Palenochtha minor* (AMNH 35451, anterior after Gunnell, 1989; Palaechthonidae?). H, *Picrodus silberlingi* (AMNH 35456, incisor after Szalay and Delson, 1979). Scales = 1 mm.

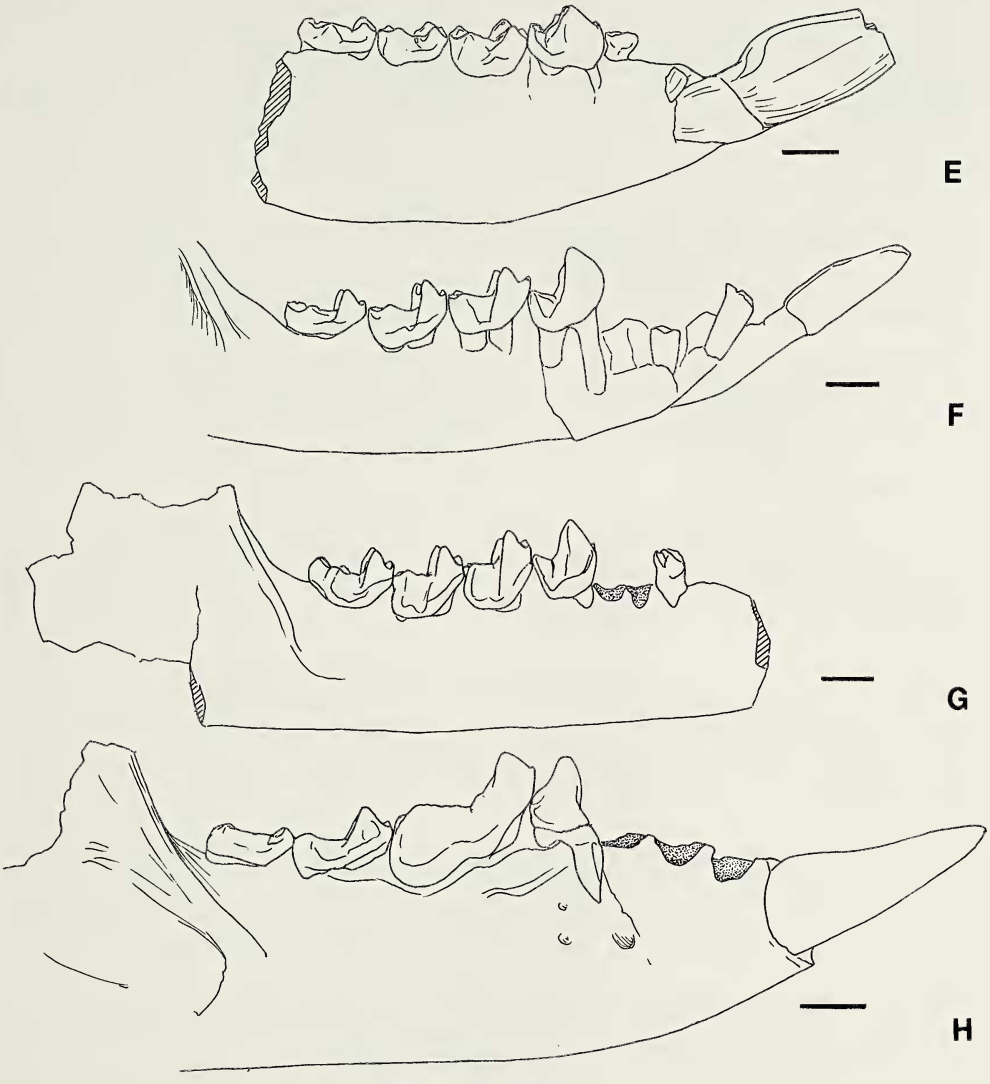

Fig. 3.—Continued.

improbable reversals or autapomorphies than other arrangements. Nonetheless, the high degree of homoplasy, including multiple convergent autapomorphies, required in both of the two shortest trees does not lend particular confidence to either one, and additional anatomical evidence is probably needed to resolve these relationships better.

When first described, *Micromomys* and *Tinimomys* were assigned to the Paromomyidae, tribe Micromomyini (Szalay, 1973, 1974). Bown and Rose (1976; Rose and Bown, 1982) used a more restricted concept of Paromomyidae, and transferred *Micromomys, Tinimomys,* and several other taxa formerly included in Paromomyidae to the Microsyopidae, an assignment followed by Fox (1984) and Gunnell (1989). More recent studies have suggested that Micromomyini diverged

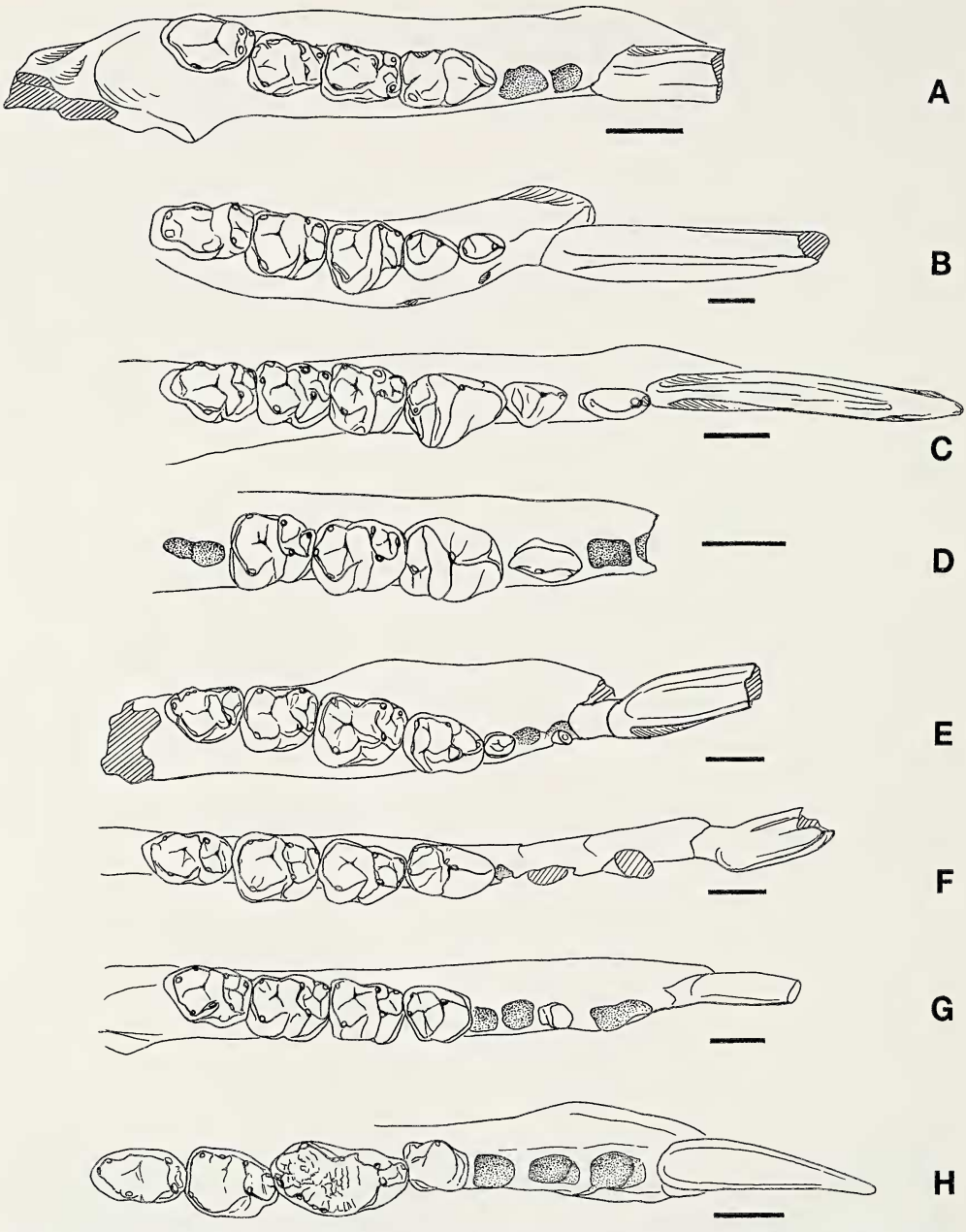

Fig. 4.—Plesiadapiform lower dentitions in occlusal view; same specimens as in Fig. 3. A, *Picromomys petersonorum,* n. gen. and sp.; B, *Ignacius fremontensis*; C, *Tinimomys graybulliensis*; D, *Micromomys antelucanus*; E, *Niptomomys doreenae*; F, *Navajovius kohlhaasae*; G, *Palenochtha minor*; H, *Picrodus silberlingi.* Scales = 1 mm.

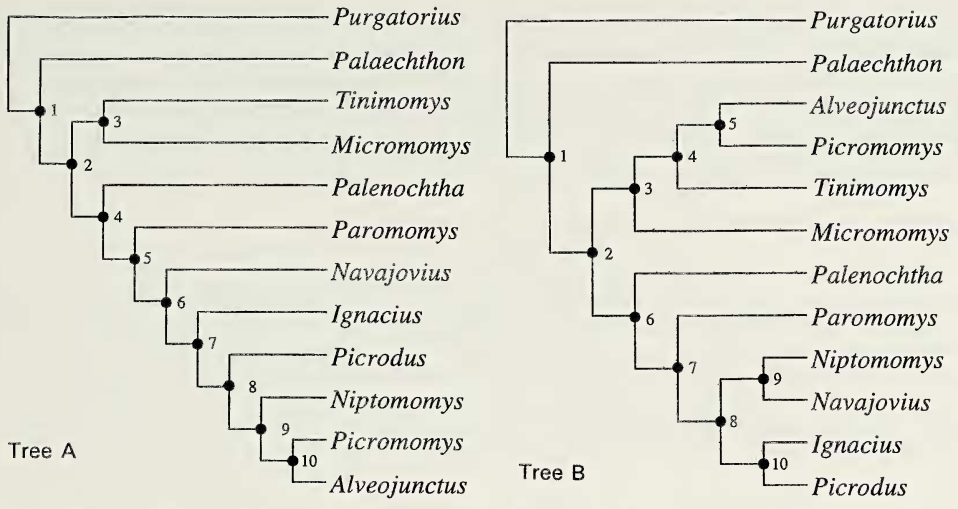

Fig. 5.—Possible relationships among picromomyids and some other plesiadapiforms: the two shortest trees based on lower dental characters given in Appendices 1 and 2, resulting from an exhaustive search using the implicit enumeration algorithm of Hennig86, which finds all trees of minimal length (Farris, 1988). Tree length = 72, consistency index = 0.48, retention index = 0.53. Ordering the characters did not change the tree topologies. Character optimization was performed using CLADOS (Nixon, 1992).

Nodes in tree A are supported by the following synapomorphies (change is from 0 to 1 for binary characters; state indicated for multistate characters): node 1—5, 7, 8(1); node 2—12(1); node 3 (Micromomyidae)—4, 10, 20, 24, 28; node 4—23; node 5—18(1), 21, 22; node 6—4, 12(2), 19; node 7—6(1), 16, 17; node 8—9, 18(2); node 9—2, 12(1–reversal), 13(1), 23 (0–reversal), 27, 29; node 10 (Picromomyidae)—10, 11, 14, 21 (0–reversal), 28. Autapomorphies required in this tree are: *Palaechthon*—21, 27; *Tinimomys*—2, 6(2), 13(2), 15(2), 18(1), 25, 28, 29; *Micromomys*—8(0–reversal); *Palenochtha*—2; *Paromomys*—8(0–reversal), 13(2), 25, 26; *Navajovius*—3, 23(0–reversal), 27; *Ignacius*—2, 6(2), 8(2), 13(2), 14, 21 (0–reversal), 25; *Picrodus*—8(2), 20, 26; *Niptomomys*—3, 4(0–reversal), 16 (0–reversal); *Picromomys*—6(2), 15(1), 20, 22(0–reversal), 26; *Alveojunctus*—12(0–reversal), 13(2), 15(2).

Nodes in tree B are supported by the following synapomorphies: nodes 1 and 2 (same as tree A); node 3—4, 10, 20, 28; node 4—2, 6(2), 13(2), 15(2), 18(1), 29; node 5 (Picromomyidae)—11, 14, 16, 17, 18(2), 19, 27; node 6—23; node 7—18(1), 21, 22; node 8—4, 12(2), 19; node 9 (Microsyopidae)—3(2), 23(0–reversal), 27; node 10—8(2), 16, 17. Taxa whose required autapomorphies differ on tree B: *Alveojunctus*—12(0–reversal), 20 (0–reversal); *Picromomys*—9, 13(1), 15(1–reversal?), 26; *Tinimomys*—24, 25; *Micromomys*—8(0–reversal), 24; *Niptomomys*—2, 4(0–reversal), 6, 9, 12(1–reversal), 13, 17, 18(2), 29; *Navajovius*—none; *Ignacius*—2, 6(2), 13(2), 14, 21 (0–reversal), 25; *Picrodus*—9, 18(2), 20, 26.

from other plesiadapiforms early in their history (Fox, 1984; Beard and Houde, 1989) and belong to a clade, the Micromomyidae, separate from other families (Beard, 1993; Rose et al., 1993). This conclusion is corroborated by the cladistic analysis presented here, but formal grouping of Micromomyidae and Picromomyidae in a higher taxon Micromomyiformes Beard, 1993, is premature from the evidence currently available (see also MacPhee et al., 1995).

Both picromomyid genera were very small plesiadapiforms, and *Picromomys* was especially diminutive (~10 g), approaching the minimum known size for mammals. Plesiadapiforms are dentally reminiscent of various extant diprotodontian marsupials such as petaurids, burramyids, and phalangerids (Cartmill, 1974). In this respect *Picromomys* and *Tinimomys* are particularly convergent on the tiny diprotodont *Acrobates*. The latter also has a hypertrophied and procumbent medial

incisor, behind which are two peg-like teeth, followed by two premolariform teeth with tall trigonids and low-crowned molars with broad talonid basins. *Acrobates* is one of the smallest known marsupials, weighing only 12–14 g; it feeds on insects, larvae, and nectar (Nowak, 1991)—a diet constrained by its dental morphology and small body size. The same constraints suggest that the diet of *Picromomys* was probably very similar.

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APPENDIX 1

Description of Characters Used in Phylogenetic Analysis

Characters were polarized with respect to *Purgatorius* as the outgroup, using 0 as the primitive state and 1 or 2 for derived states. Characters 6, 8, 12, and 18 were treated as ordered; all others are unordered. Intraspecifically variable traits were coded according to the predominant character state. Autapomorphic characters known to be present in only one of the genera analyzed are excluded from the analysis.

1. I_1 small to moderate (0); hypertrophied (1). Although incisors have not been described for *Purgatorius,* alveoli suggest that its medial incisor was relatively less enlarged than in other plesiadapiforms.

2. I_1 somewhat inclined (0); strongly procumbent to horizontal (1).

3. I_1 laterally compressed (1); laterally compressed and lanceolate (2). The primitive state is unknown; both states observed could be derived, hence no taxa are scored as 0.

4. I_2 present (0); absent (1). Scoring of this character is obviously dependent on the homologies of the anterior dentition, which are equivocal in most taxa used here. See Appendix 2 for dental formulae used in this analysis.

5. I_3 present (0); absent (1). This character is subject to the same ambiguity as character 4, but relative tooth sizes support the derived state in most plesiadapiforms.

6. Canine moderately large: alveolus usually $\geq$, or crown higher, than I_2 and $P_{1\text{ or }2}$ (0); noticeably reduced, smaller than adjacent teeth (1); absent (2). Same ambiguity as character 4. In addition, relative size is often difficult to judge due to poor preservation.

7. P_1 present (0); absent (1). Equivocal in *Palenochtha* because of conflicting interpretations of the dental formula.

8. P_2 two-rooted (0); one-rooted (1); absent (2). Same ambiguity as character 4.

9. P_3 two-rooted (0); one-rooted (1).

10. P_4 about the size of M_1 or smaller (0); larger than M_1 (1).

11. P_4 talonid shorter than trigonid (0); about as long as trigonid (1).

12. P_4 trigonid with distinct paraconid (0); with paracristid with or without

vestigial paraconid (1); with protoconid only, no trace of paraconid or paracristid (2). Ambiguous in *Picromomys,* owing to wear and/or morphology.

13. P_4 talonid narrow (0); broad but without basin (1); broad and with basin (2).

14. P_4 cristid obliqua joins trigonid near its midline axis (0); near buccal margin of trigonid (1). Although coded "0," *Paromomys* displays a somewhat intermediate condition.

15. P_4 talonid with hypoconid and weak entoconid (0); entoconid absent (1); with enlarged entoconid (2).

16. P_4 and molar hypoflexids distinct (0); shallow to absent (1). Characters 13, 14, and 16 are often but not always correlated.

17. P_4 and molar trigonids relatively tall and erect (0); lower and strongly anteriorly inclined (1).

18. Molars relatively high crowned (0); of moderate height (1); very low crowned (2). Scoring was based on mean index of M_2 trigonid height/length, with three arbitrary divisions: $\geq$ 0.79 (0), 0.60–0.71 (1), $\leq$ 0.53 (2).

19. Anterobuccal cingulids well developed (0); weak or absent (1).

20. Molar trigonids transversely broad (0); transversely compressed (1). Intermediate condition in *Palenochtha.*

21. Molar paraconids moderately reduced (0); greatly reduced or absent (1). The utility of this character, except for extreme manifestations, is dubious because of its intraspecifically variable and continuous nature.

22. M_1 mesoconid weak (0); absent (1). Intraspecifically variable in *Tinimomys* and perhaps others.

23. M_{1-2} hypoconulids prominent (0); small or indistinct (1). Ambiguous state in *Micromomys* due to intermediate expression.

24. Molar talonid cusps and crests peripheral (0); set in from margin as a result of basal inflation (1).

25. M_3 third lobe not expanded (0); expanded (1).

26. Enamel smooth (0); crenulated to a variable degree (1).

27. P_4 trigonid without metaconid (0); with metaconid (1).

28. M_{1-2} hypoconulids central in position (0); distinctly closer to entoconid (1).

29. M_{1-2} without entoconid notch (0); with distinct notch between hypoconulid and entoconid (1). Variable in *Niptomomys* examined.

APPENDIX 2

Character Matrix Used for Phylogenetic Analysis

Characters deemed too ambiguous to score are indicated by "a" and were scored as missing data ("?") for the analysis. At right is the lower dental formula assumed in this analysis. Where tooth number varies within a genus, the most primitive known formula is given.

Purgatorius	0??00	00000	00000	00000	00000	0000	3-1-4-3
Palaechthon	???01	01100	00000	00000	10000	0100	2-1-3-3
Palenochtha	11101	01100	01000	0000a	00100	0000	2-1-3-3
Picromomys	11111	21111	11111	11211	00000	1111	1-0-3-3
Alveojunctus	?????	????1	10212	11210	0?00?	?111	?
Paromomys	10?01	01000	01200	00100	11101	1000	2-1-3-3
Ignacius	11111	21200	02210	11110	01101	0000	1-0-2-3
Navajovius	10211	01100	02000	00110	11000	0100	1-1-3-3
Micromomys	10111	01001	01000	00001	00a10	0010	1-1-3-3
Tinimomys	11111	21101	01202	00101	00011	0011	1-0-3-3
Niptomomys	11211	11110	01100	01210	11000	0101	1-1-3-3
Picrodus	10??1	?1210	02000	11211	11100	1000	?-?-2-3